# Bilateral Asymmetry in the Shell Morphology and Microstructure of Early Ontogenetic Stages of *Anomia simplex*

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**Abstract.** Scanning electron microscopic examination of the valves of *Anomia simplex* larvae and postlarvae provides details of bilateral asymmetry in shell morphology and microstructure. Central provincular denticles and larger anterior and posterior hinge teeth develop in both valves. The umbo of the left valve becomes increasingly prominent with larval development, whereas no umbo is evident in the right valve. Thus, right and left valves of the prodissoconch differ markedly in height.

In the left valve of the dissoconch, union of antero- and posterodorsal shell margins above the hinge causes lateral, exterior displacement of the umbo. The internal ligament extends ventrally to the right valve. Thin antero- and posterodorsal shell margins of the right valve extend centrally against the substrate and eventually unite exterior to the ligament. An increasingly larger byssal foramen, with a flexible, organic covering, is formed in the right valve.

The outer layer of the left valve of the dissoconch is foliated calcite, whereas the outer layer of the right valve is composed of short, calcitic prisms. Inner shell layers consist of crossed lamellar and complex crossed lamellar microstructure, as well as myostracal prisms.

## Introduction

The Anomiidae are noted for striking dissimilarity of the right and left valves. Bilateral asymmetry of the shell, which ultimately is an adaptation for secure attachment to the substrate (Yonge, 1977), begins in early larval stages. A prominent umbo characterizes the highly convex left valve; in contrast, an umbo is not apparent in the nearly flat right valve (Stafford, 1912; Miyazaki, 1935; Lebour, 1938; Jørgensen, 1946; Sullivan, 1948; Loosa-

noff *et al.*, 1966; Chanley and Andrews, 1971; Yonge, 1977; Le Pennec, 1978; Booth, 1979). Larval hinge dentition in the Anomiidae is taxodont; each valve has a series of small, central teeth and 2–5 anterior and posterior teeth, which enlarge during the larval period (Jørgensen, 1946; Yonge, 1977; Le Pennec, 1978, 1980). In some anomiids, formation of additional anterior and posterior provincular teeth in the left valve results in bilateral asymmetry of the larval hinge (Le Pennec, 1978, 1980).

After metamorphosis, the right (lower) valve develops an expansive foramen through which a calcified byssus attaches to the substrate (except in some free-living anomiids), while the left valve shows heightened shell growth along the antero- and posterodorsal margins, which eventually unite dorsally, above the hinge (Taylor *et al.*, 1969; Yonge, 1977; Le Pennec, 1978; Prezant, 1984). This "supradorsal" growth in the left valve leads to lateral displacement of the umbo and ventral extension of the ligament to the dorsal region of the crurum of the right valve (Yonge, 1977). [Crurum, used in the sense of Beu (1967) and Yonge (1977, 1980), refers to the prominent chondrophore in the right valve of the Anomiacea.]

In some anomiids, calcitic foliated microstructure is the principal structural type in both right and left adult valves, while in other anomiids, the left valve is predominantly foliated calcite, and the right valve is primarily prismatic calcite (Beu, 1967; Kobayashi, 1969; Taylor *et al.*, 1969; Waller, 1978; Yonge, 1980). An inner layer of aragonitic crossed or complex crossed lamellar microstructure surrounds the muscle scars in the left valve and the byssal foramen and muscle scar in the right valve (Taylor *et al.*, 1969; Waller, 1978). As in other bivalves, the myostracum is prismatic aragonite (Taylor *et al.*, 1969; Waller, 1978; Carter, 1980a).

The present scanning electron microscopic study pro-

vides a comprehensive description of the bilateral asymmetry in shell morphology and microstructure of early ontogenetic stages of *Anomia simplex* d'Orbigny, the common jingle shell of the western Atlantic. Details of shell morphological development are documented with micrographs of sequential stages. Comparison of early shell morphology in various North Atlantic anomiids reveals features useful in studies concerning species identification and taxonomy. A summary of the bilateral asymmetry in shell morphology and microstructure of early ontogenetic stages of four other common, inequivalve pteriomorphs from the North Atlantic is included.

## Materials and Methods

Adult specimens of *Anomia simplex* were collected in Wachapreague Inlet, Virginia, and were spawned by raising the ambient water temperature from 25 to 30°C. Larvae were cultured in filtered (50 $\mu$m mesh) baywater (salinity = 32–34 ‰; temperature = 22.4–32.0°C) using standard techniques (Loosanoff and Davis, 1963). When larvae approached metamorphosis, a layer of eggshells was placed at the bottom of the culture tank. Spat on the eggshells and on the sides of the tank were attached loosely and were removed easily for sampling.

Samples from larval cultures were treated with a 5.25% solution of sodium hypochlorite for 10 min to remove soft tissues (after Rees, 1950); disarticulated valves were rinsed with distilled water. Soft tissues were dissected from postlarval specimens with a small brush. The pliable nature of postlarval right valves required careful placement as shells were mounted on silver tape. All specimens were coated with approximately 600 Å of gold-palladium and were documented with an ETEC Autoscan scanning electron microscope. Positioning disarticulated valves with selected points on the shell margin aligned in a plane normal to the electron beam of the microscope resulted in consistent orientation for documentation of shape. Photographs of a standard grid at the same magnification as each shell specimen provided accurate dimensions of shell features. Shell length is defined as the greatest anteroposterior shell dimension; shell height refers to the greatest measurement perpendicular to the hinge line. Terminology for juvenile and adult ligament components is that of Yonge (1977, 1980). Microstructural terminology is taken from Carter (1980b) and Carter and Clark (1985). Microstructural varieties of inner shell layers were determined by examination with reflected light and scanning electron microscopy.

## Results

Right and left valves of the prodissoconch I range from 75 to 80 $\mu$m long ($\overline{x} \pm$ SD = 76.4 ± 2.1; n = 10). The inequivalve nature of *Anomia simplex* is evident at a
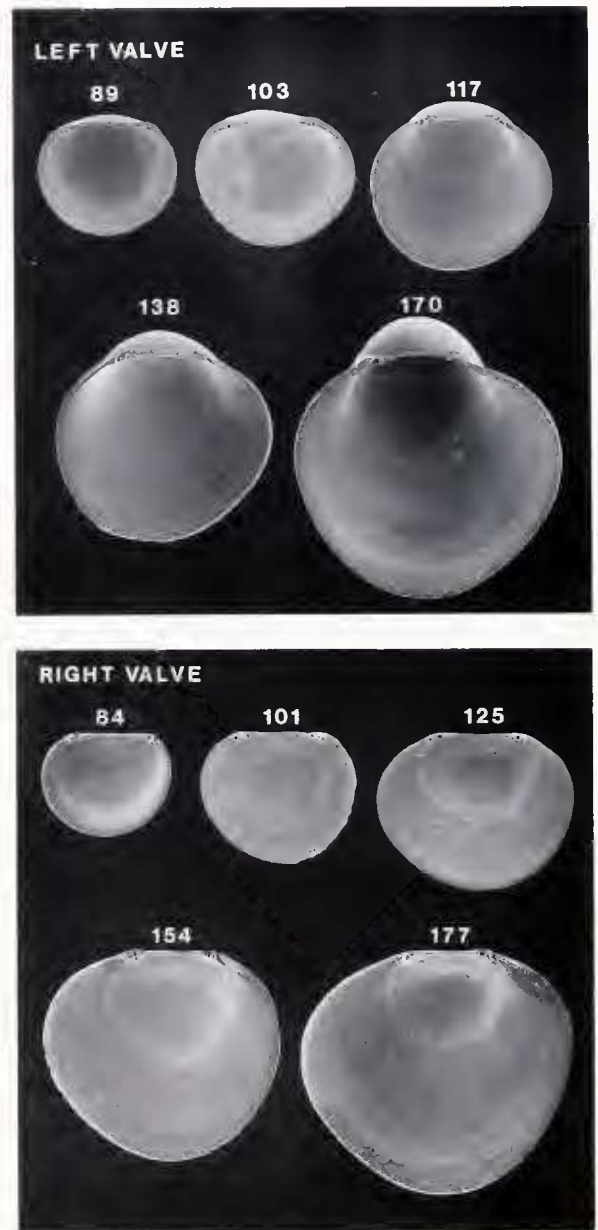


Figure 1.   Scanning electron micrographs of disarticulated valves of *Anomia simplex* larvae. Numbers indicate shell lengths in $\mu$m.

shell length of 85–90 $\mu$m, as a result of formation of a low, rounded umbo in the left valve (Figs. 1, 2). Left valves are equidimensional at approximately 140 $\mu$m; shell height exceeds shell length during late larval stages. In the right valve, shell height is less than shell length throughout the larval period (Fig. 1).

Provinculum length ranges from 54 to 62 $\mu$m ($\overline{x} \pm$ SD = 57.1 ± 2.8 $\mu$m; n = 18). A series of minute, irregular denticles extends across the central portion of the provinculum in early larval valves; these interlocking denticles are slightly larger and more distinct in late larval stages (Fig. 2). Pairs of teeth, which also grow with larval devel-
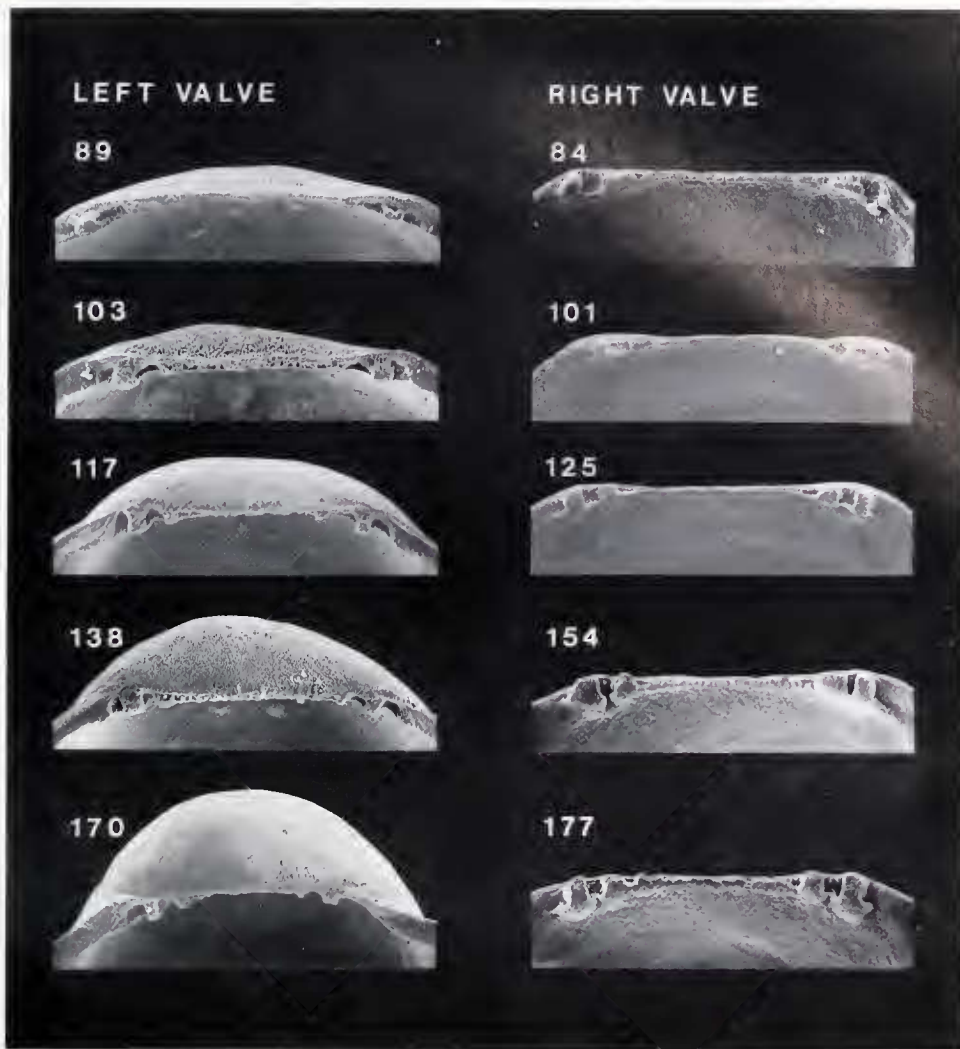
**Figure 2.** Scanning electron micrographs of the hinge of disarticulated valves of *Anomia simplex* larvae seen in Figure 1. Numbers indicate shell lengths in μm.

opment, form at the anterior and posterior extremes of the provinculum (Fig. 2). Articulation of the hinge teeth shifts gradually from a lateral to a dorsoventral orientation; in the right valve at a length of approximately 155 μm, anterior and posterior provincular teeth extend dorsally over the shell margin (Fig. 2).

The first morphological evidence of postlarval development is formation of a ligament pit at a shell length of approximately 190 μm, at which size central provincular denticles are mostly obliterated (Figs. 3, 4). Lengths of right and left valves are equal at this stage, but the left valve is approximately 24 μm higher than the right valve. Supradorsal growth of the left valve begins at a shell length of approximately 240 μm (Fig. 3). Bold margins of foliated microstructure expand first dorsally and then centrally across the umbo (Figs. 3, 5). By a shell length of approximately 1050 μm, supradorsal extensions are as high as the umbo, and anterior and posterior provincular

teeth are obsolete (Figs. 3, 4). Anterior and posterior shell margins extend approximately 200 μm above the hinge before they unite centrally (Fig. 6). Supradorsal union of the antero- and posterodorsal shell extensions is complete in specimens approximately 1600 μm long (Fig. 3). The gap between the two margins is no longer visible in juvenile specimens approximately 5.5 mm long (Figs. 7, 8). At this size, several adult shell morphological features are recognizable, including the laterally displaced umbo, the differentiated inner and outer layers of the ligament, and three central muscle scars of myostracal prisms (Figs. 7–9). The inner layer surrounding the muscle scars is mostly fine and irregular complex crossed lamellar aragonite (Figs. 8, 10). The principal microstructural component of the left valve is foliated calcite (Figs. 7, 11).

A semicircular ligament pit, which is approximately 21 μm long, lies in the center of the hinge of the right valve of early postlarval specimens ranging from 190 to
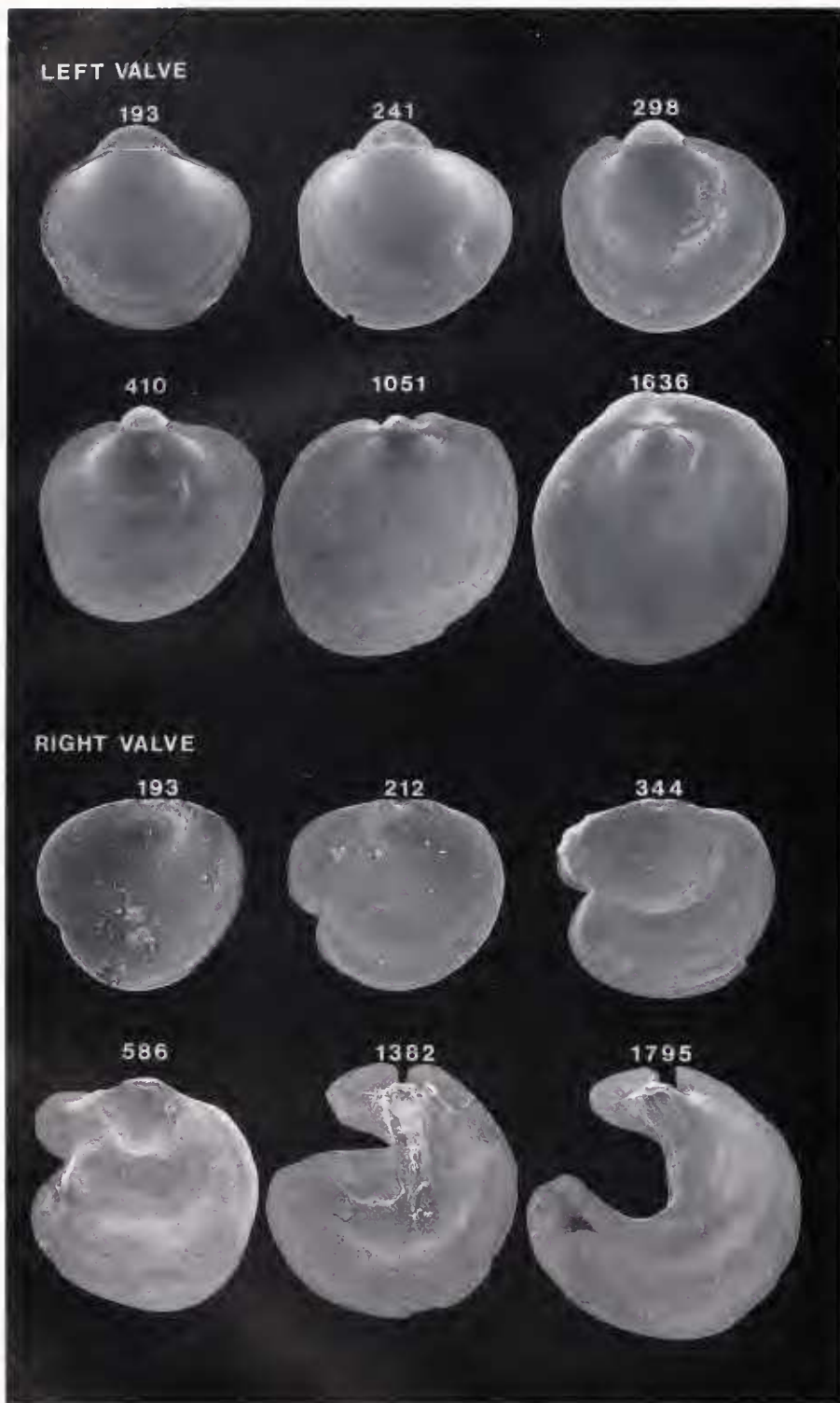
**Figure 3.**   Scanning electron micrographs of disarticulated valves of *Anomia simplex* postlarvae. Numbers indicate shell lengths in μm.

240 μm long (Figs. 3, 4). In specimens approximately 350 μm long, anterior and posterior provincular teeth are obscured, and the ligament pit is positioned dorsally to the hinge (Fig. 4). At a shell length of 500–700 μm, the anterodorsal and anteroventral shell margins are united immediately adjacent to the byssal notch but are separated anteriorly by the byssal foramen (Figs. 3, 12, 13). At a shell length of 700–900 μm, the posteroventral re-
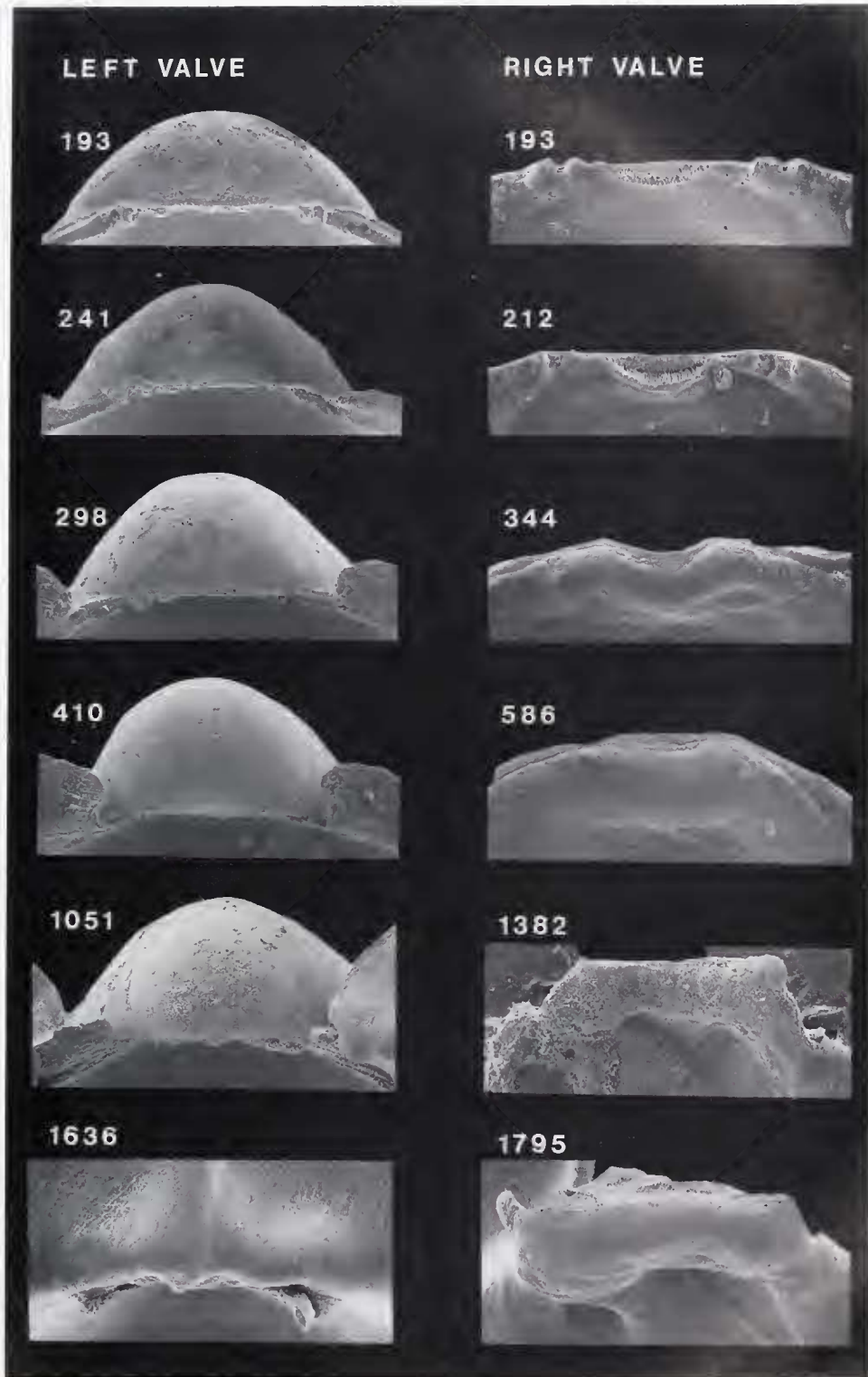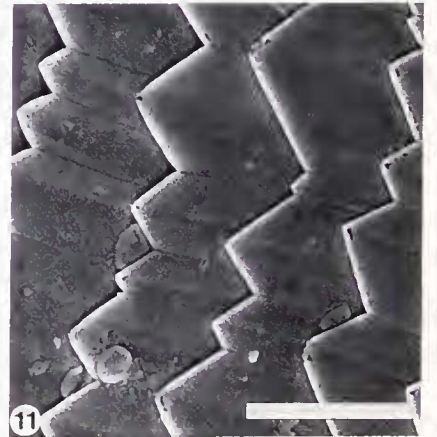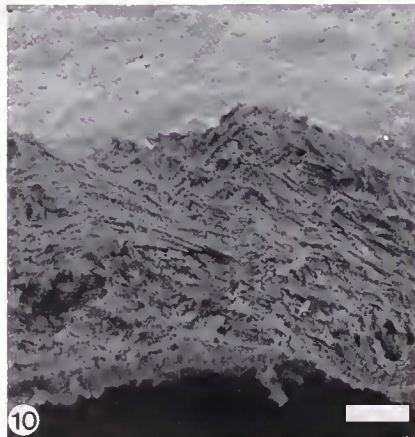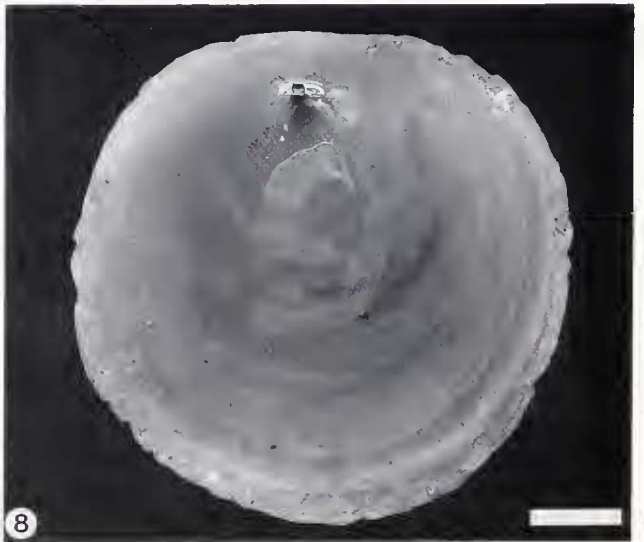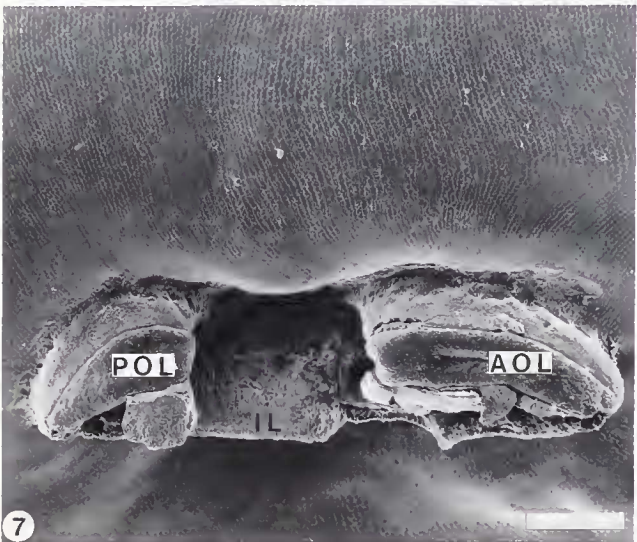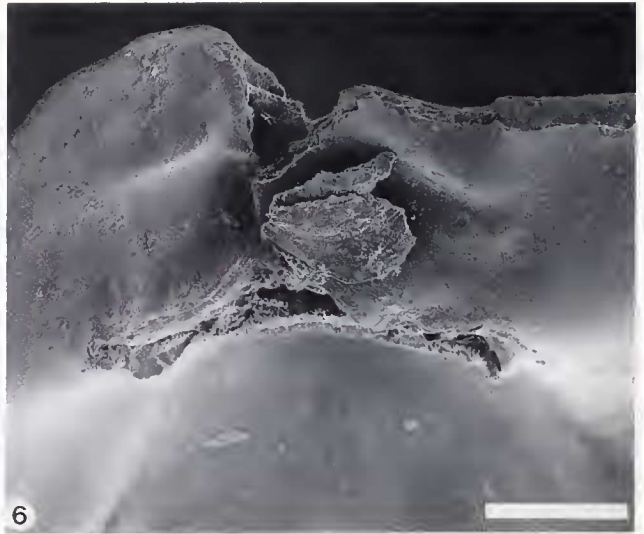
**Figure 4.** Scanning electron micrographs of the hinge of disarticulated valves of *Anomia simplex* post-larvae seen in Figure 3. Numbers indicate shell lengths in μm.

gion of the byssal foramen is covered by a flexible, organic sheet, which is continuous with the adjacent prismatic outer shell layer and is mostly calcified along the anterior edge (Figs. 14–16). Expansion of the anterodorsal and anteroventral shell margins enlarges the byssal foramen anteriorly, while resorption of the shell extends
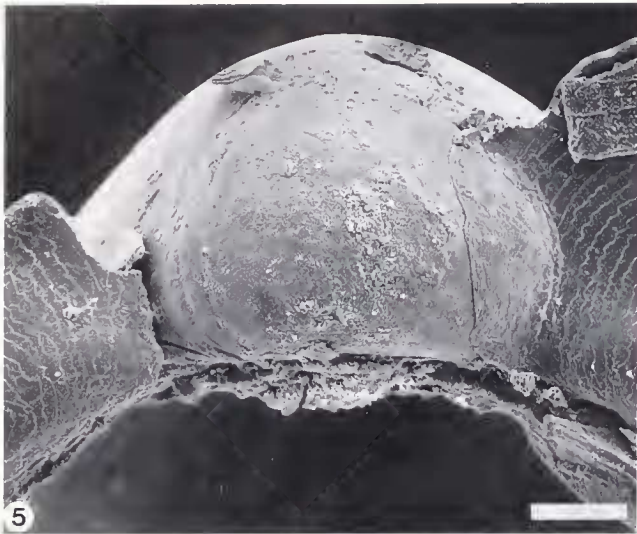
**Figures 5–11.** Scanning electron micrographs of the left valve of postlarval specimens of *Anomia simplex.*

**Figure 5.** Posterior expansion of the anterodorsal shell margin across the umbo. Scale bar = 20 μm.

**Figure 6.** Supradorsal extension of anterior and posterior shell margins. Scale bar = 100 μm.

**Figure 7.** Ligament and supradorsal shell region after union of anterodorsal and posterodorsal shell margins in a juvenile specimen. Note the vertical pattern of outcropping edges of folia on the growth surface of the supradorsal shell region. Scale bar = 100 μm. POL, posterior outer layer of the ligament; AOL, anterior outer layer of the ligament; IL, inner layer of the ligament.

the foramen in a posterior direction (Fig. 14). The extent of the covering, across the posteroventral portion of the foramen, remains constant during shell growth (Fig. 14).

A calcitic outer layer of short prisms comprises most of the right valve of the early dissoconch (Fig. 17). An inner layer, which is mostly crossed lamellar aragonite, surrounds the byssal foramen and single muscle scar (Fig. 18). No obvious surface features were observed on a narrow band of the inner shell layer closest to the byssal foramen; a fractured section of this region is illustrated in Figure 19. No foliated microstructure was observed during thorough examinations of the right valve of postlarval specimens at several developmental stages. As the crurum increases in thickness and complexity, adjacent antero- and posterodorsal shell margins extend dorsally and centrally in a thin shell layer and are united at a shell length of 8.0 mm (Figs. 20, 21). In late postlarval stages, the crurum is comprised of several prismatic layers that overgrow and obscure the prodissoconch (Figs. 22, 23).

## Discussion

Yonge (1977) described development of the ligament in the left valve of anomiids as a rounding of the anterior and posterior outer layers over the dorsal side of the inner layer. He pointed out that, in *Anomia*, the supradorsally extended mantle lobes and antero- and posterodorsal shell margins unite, but anterior and posterior outer layers of the ligament remain separate. As a result of intense growth in the supradorsal region of the left valve, the outer layers of the ligament lie laterally interior to the inner layer (Yonge, 1977).

Development of the ligament in the right valve of anomiids has been poorly understood; however, examination of postlarval shells of *Anomia simplex* in the present study reveals a developmental process similar to that in the left valve. In the right valve, lateral (interior) displacement of the prodissoconch and dorsally extending ligament gives rise to the crurum (Fig. 3). Anterior and posterior outer layers of the ligament extend centrally around the crurum and thus are positioned laterally exterior to the inner layer and in vertical alignment with the corresponding layers in the left valve (Fig. 22). Concealment of the prodissoconch during postlarval developmental stages is illustrated in Figure 22; layers of prisms mask the early shell and thicken the crurum.

Shell morphological changes in the left valve of *A. simplex* during postlarval stages are similar to those de-

scribed by Yonge (1977) for *Pododesmus cepio* (Gray). Early dissoconch growth is uniform along anterior, posterior, and ventral margins. Heightened dorsal extension followed by central growth across the umbo results in supradorsal union of shell margins, displacement of the umbo to an exterior position, and dorsoventral orientation of the ligament.

Shell morphological changes in the right valve of *A. simplex* during initial postlarval developmental stages also are similar to those described by Yonge (1977) for *P. cepio* in that the byssal foramen is formed between the anterodorsal and anteroventral dissoconch regions, which are united posteriorly. In the present study, documentation of further postlarval developmental stages in *A. simplex* reveals that as adjacent shell margins expand, the byssal foramen is lengthened anteriorly, while shell resorption extends the foramen posteriorly. In late postlarval developmental stages, the anterodorsal shell margin continues to expand slightly, but exaggerated growth of the anteroventral margin substantially increases the size of the byssal foramen (Figs. 3, 21). Further enlargement of the byssal foramen to the adult size occurs by shell resorption (Jackson, 1890; Yonge, 1977). Similar expansion of the adult byssal notch is found in the pectinid *Pedum spondyloideum* (Gmelin) (Yonge, 1967; Waller, 1972).

A sheet of decalcified prisms covers the posteroventral region of the byssal foramen in postlarvae of *A. simplex* (Figs. 14–16). A similar structure has been described in some of the Propeamussiidae (Waller, 1984), a family with close ancestry to the Anomiacea (Waller, 1978). The covering in these glass scallops is an extension of the prismatic outer layer of the right valve; with growth of the byssal fasciole, the covering becomes "an appliqué on the surface of the fasciole" (Waller, 1984).

Several features of the shell morphology and internal anatomy of adult *A. simplex* and *Anomia ephippium* L., the common jingle shell of Europe, are similar (Yonge, 1977, 1980). Some authors (*e.g.*, Fischer-Piette, 1973; Porter, 1974; Rios, 1985) have listed these two species as synonymous, while others (*e.g.*, Dall, 1898; Olsson and Harbison, 1953; Abbott, 1974) preserve separate species. Comparison of larval and early postlarval shell morphological features of *A. simplex* with those of *A. ephippium*, described by Le Pennec (1978, 1980), suggests similarity in the two species. Shell length during the straight-hinge developmental stage is 75 μm in *A. ephippium* (Le Pen-

**Figure 8.** Shell after supradorsal union of anterior and posterior shell margins; specimen is the same as that in Figure 7. Scale bar = 1.0 mm.

**Figure 9.** Fracture section through the prismatic layer of the dorsal muscle scar. Scale bar = 5 μm.

**Figure 10.** Fracture section through the inner shell layer in the region adjacent to the dorsal muscle scar; note complex crossed lamellar microstructure. Scale bar = 5 μm.

**Figure 11.** Folia of the interior surface of the outer shell layer. Scale bar = 5 μm.
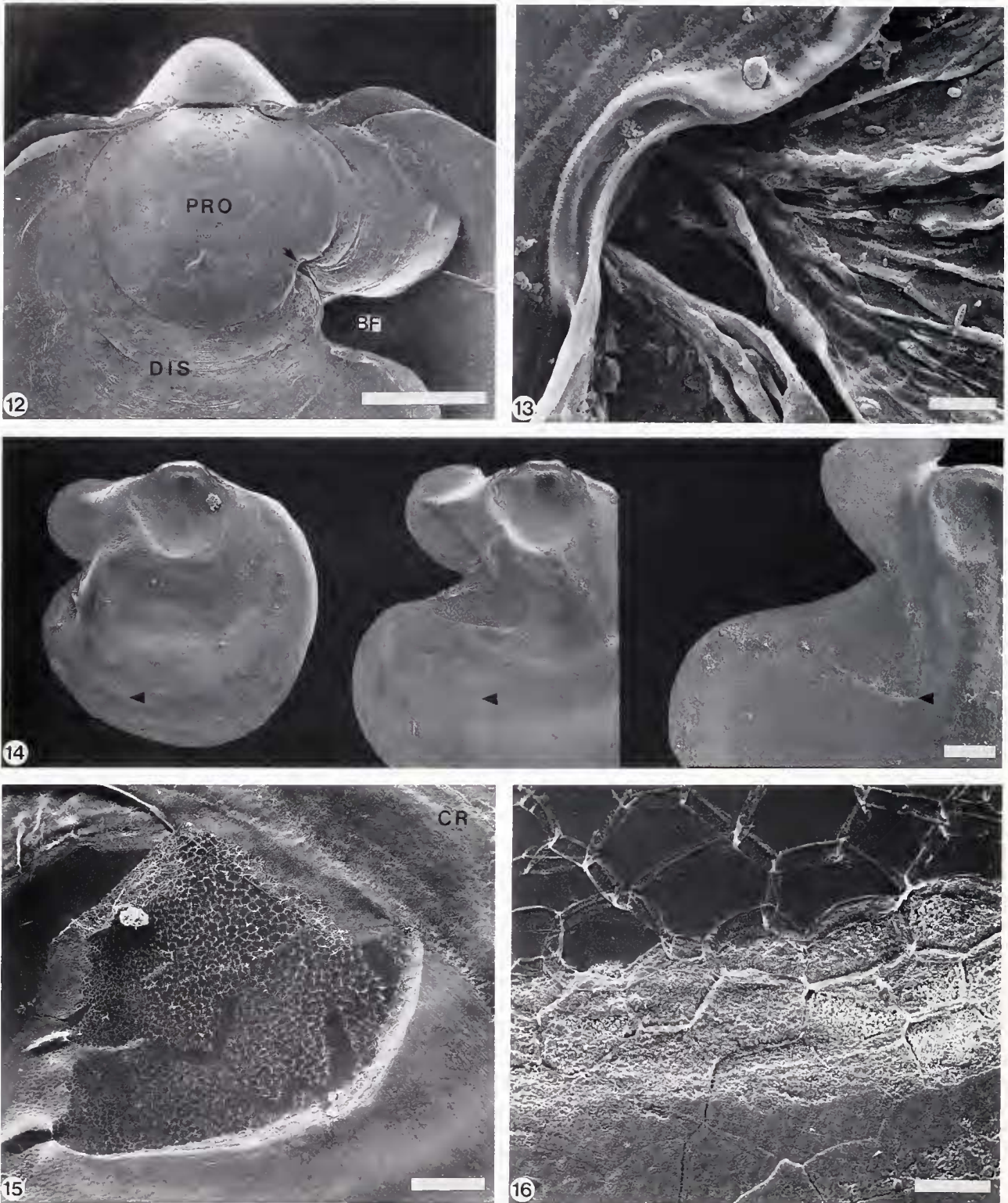
Figures 12–16.  Scanning electron micrographs of the right valve of postlarval specimens of *Anomia simplex*.

Figure 12.  Exterior surface of a shell 620 μm long. Arrow marks region of detail in Figure 13. Scale bar = 100 μm. PRO, prodissoconch; DIS, dissoconch; BF, byssal foramen.

Figure 13.  Prismatic secretions at the byssal notch. Scale bar = 5 μm.

Figure 14.  Interior surface at three sequential stages to illustrate enlargement of the byssal-foramen covering by shell resorption. Arrow marks the same spot on the three specimens, which are figured to scale. Scale bar = 100 μm.

nec, 1978); initial shell length of *A. simplex* ranged from 75 to 80 μm in the present study, although individuals as small as 58–60 μm long have been reported (Loosanoff *et al.*, 1966; Chanley and Andrews, 1971). Le Pennec (1978) described formation of an early umbo in the left valve of *A. ephippium* at a length of 100 μm and prominence of the umbo at a length of 110 μm. In specimens of the left valve of *A. simplex* depicted in Figures 1 and 2, an umbo is evident at a shell length of 89 μm and is well-developed at a shell length of 117 μm. Chanley and Andrews (1971) described development of a rounded umbo in the left valve of *A. simplex* specimens 90–110 μm long. Larval hinge dentition in both species consists of a central region of denticles and a pair of larger teeth at the anterior and posterior ends of the provinculum. In the left valve of *A. ephippium*, a third tooth is added at the anterior and posterior extremes of the hinge at a shell length of approximately 100 μm (Le Pennec, 1978, 1980). A third tooth is evident in the same position in *A. simplex* when shells are 117 μm long (Fig. 2), but these new teeth are not well-developed in either species. In *A. ephippium*, formation of a ligament pit occurs when shell height and shell length average 190 μm (Le Pennec, 1978). In specimens of *A. simplex* in the present study, a ligament pit is formed in shells 193 μm long; these post-larvae also are equidimensional. Previous workers reported that metamorphosis in *A. simplex* occurred when animals were 180–215 μm long (Loosanoff *et al.*, 1966; Chanley and Andrews, 1971). Finally, at a shell length of 250 μm, right and left valves of *A. ephippium* differ by 60 μm in length and by 70 μm in height (Le Pennec, 1978). Inequality of dimensions of right and left valves of the dissoconch of *A. simplex* is illustrated in an articulated specimen approximately 485 μm long (Fig. 24). Right and left valves of this specimen differ by 70 μm in length and by 50 μm in height.

Despite similarities in shell morphologies of early ontogenetic stages in the two species, examination of shell microstructure of early stages reveals a significant difference between *A. simplex* (= *glabra*) and *A. ephippium* and a basis for taxonomic separation (Jackson, 1890). The right valve of the dissoconch of *A. simplex* is comprised largely of prismatic microstructure, and the left valve is predominantly foliated (Jackson, 1890; present study). On the other hand, both valves of the early dissoconch of *A. ephippium* are predominantly foliated; prismatic microstructure is confined to a relatively thin outer layer of the right valve (Carpenter, 1848; Jackson, 1890). Clearly, further studies are necessary to determine

the genetic distance between *A. simplex* and *A. ephippium*.

Historically, presence of a byssal notch has been a major distinguishing character used in the identification of early ontogenetic stages of anomiid species from the North Atlantic. Previously, a byssal notch was found in only the right valve of *A. simplex* and *A. ephippium*, whereas *Anomia squamula* (= *aculeata*) L. and *Anomia patelliformis* L. have a notch in both right and left valves (the notch in the left valve is shallower than the notch in the right valve) (Jackson, 1890; Ranson and Desjardin, 1941; Jørgensen, 1946; Merrill, 1962; Yonge, 1977; Le Pennec, 1978). However, data in the present study indicate that a notch sometimes occurs in the left valve of *A. simplex* (Fig. 25). Because of this variability, use of this feature for species identification may result in error.

Other details of early shell morphology of *A. squamula* and *A. patelliformis* are not well-documented. Because larval anomiids are distinctive and easily separated from other bivalve larvae by their bilateral asymmetry and conspicuous byssal notch [or pedal sinus (Yonge, 1977)], most descriptions of larval stages are limited to these two features. However, larval hinge dentition has been described for *A. squamula;* the provinculum of this species has central denticles and 3–5 larger teeth at the extremes (Jørgensen, 1946). The anterior and posterior hinge teeth of *A. squamula* are more pronounced (see Jørgensen, 1946, Fig. 162) than those of *A. simplex;* larval hinge morphology, therefore, would provide a reliable means of distinguishing these two sympatric species during planktonic stages.

Jackson (1890) described the prodissoconch of *A. simplex* (= *glabra*) as having "homogeneous" microstructure and fine commarginal lines on the exterior surface. He described the left valve of the dissoconch as "subnacreous" (foliated), with an inner "porcelaneous" region surrounding the muscle scars, and the right valve of the dissoconch as "prismatic," with a white, "porcelaneous" band around the byssal foramen. The previously reported foliated and prismatic microstructures of the outer layers are confirmed in the present study; secretion of these layers begins at the clearly delineated prodissoconch-dissoconch boundary (Figs. 12, 24, 25). In addition, reflected light and scanning electron microscopic examination of the inner shell layers has enabled categorization of the "porcelaneous" microstructure. Most of the surface of the inner shell layer of the right valve of the early dissoconch has well-defined first order lamellae, and the microstructure is distinctly crossed lamellar. Ex-

**Figure 15.** Interior surface view of the byssal-foramen covering of a specimen 1.5 mm long. Scale bar = 100 μm. CR, crurum.

**Figure 16.** Interior surface at the junction of the byssal-foramen covering and the anteroventral shell margin. Scale bar = 10 μm.
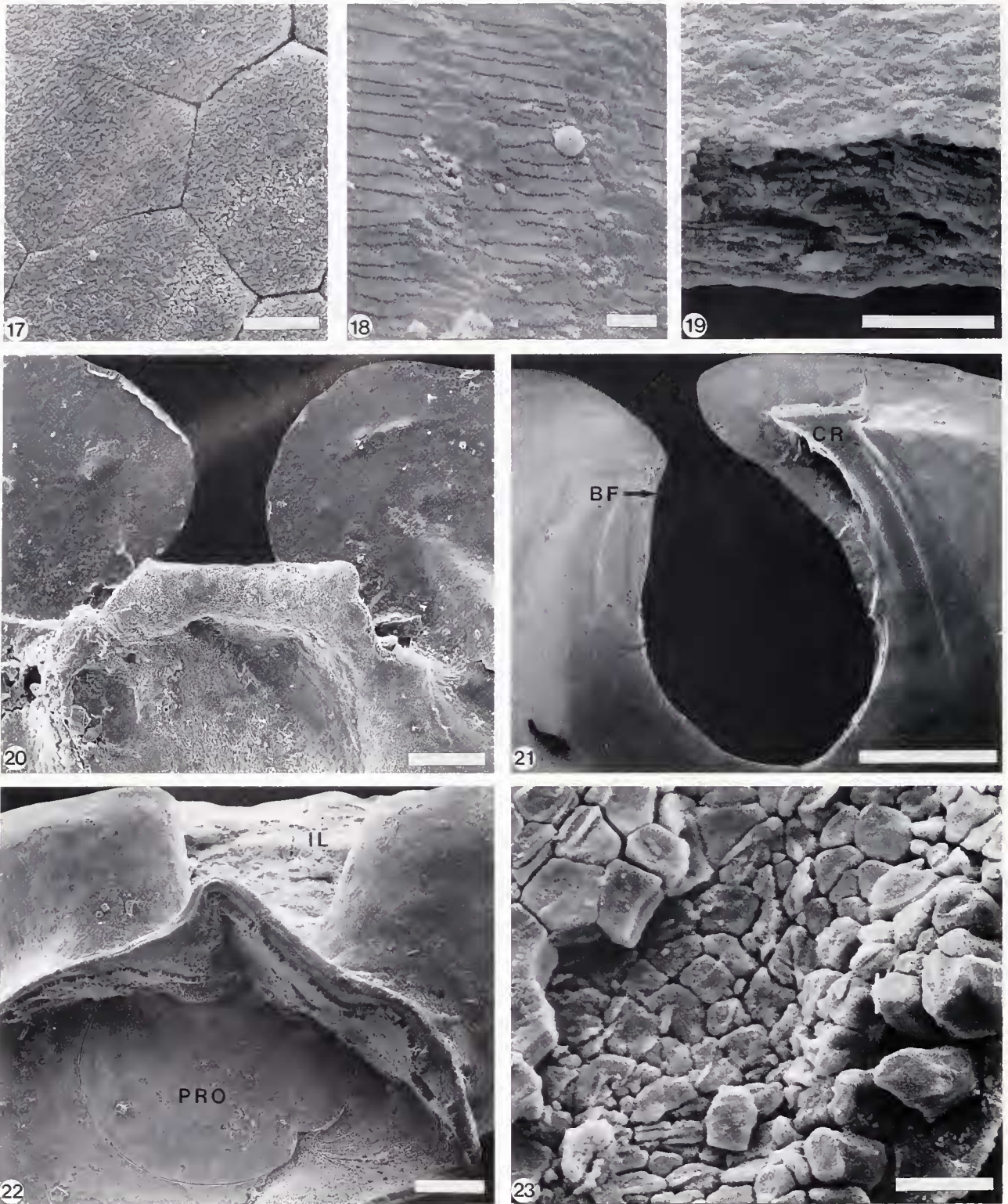
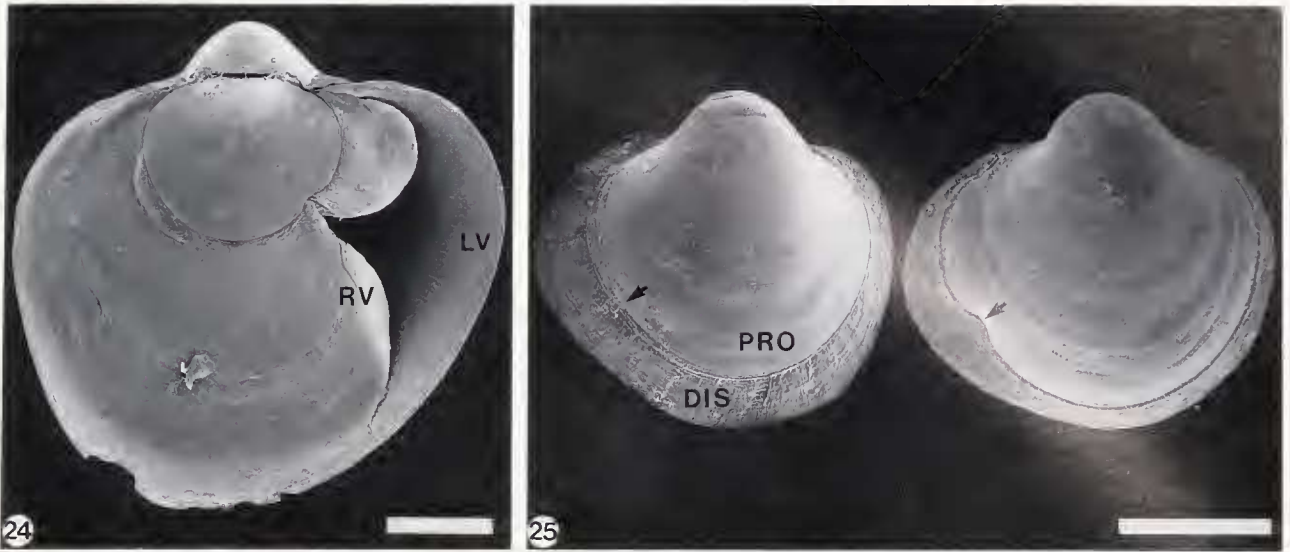Figures 17–23. Scanning electron micrographs of the right valve of postlarval specimens of *Anomia simplex.*

Figure 17. Interior surface view of the prismatic outer layer. Scale bar = 5 μm.

Figure 18. Surface view of the crossed lamellar inner layer. Scale bar = 20 μm.

Figure 19. Fracture section of a specimen 2.0 mm long through the region of the inner shell layer closest to the byssal foramen. Scale bar = 5 μm.

Figure 20. Hinge region of the right valve before supradorsal union of shell margins. Scale bar = 50 μm.

**Figures 24–25.** Scanning electron micrographs of postlarval specimens of *Anomia simplex.*
**Figure 24.** Lateral view of articulated shell. Scale bar = 100 μm. RV, right valve; LV, left valve.
**Figure 25.** Exterior surface of two left valves to show variation in byssal notch structure. Scale bar = 100 μm. PRO, prodissoconch; DIS, dissoconch.

amination of the fractured section of the interior region of this inner layer (depicted in Fig. 19) indicates a variety of complex crossed lamellar microstructure with a low dip angle (J. Carter, pers. comm.). The inner layer of the left valve of the early dissoconch has fine and irregular complex crossed lamellae.

The right valve of *A. squamula* (= *aculeata*) also is predominantly prismatic calcite (Jackson, 1890). In contrast, both valves of adult specimens of *Anomia trigonopsis* Hutton examined by Beu (1967) and of *A. ephippium* and *Anomia peruviana* d'Orbigny examined by Taylor *et al.* (1969) were mostly foliated calcite. Few studies subsequent to those conducted by Jackson (1890) have reported prismatic microstructure in the right valve in *Anomia*. Beu (1967) found that the right valve of three species of *Patro* is comprised primarily of prismatic microstructure and suggested that this character generally separates *Patro* from *Anomia*. Although *Patro* and *Anomia* have several other morphological differences in shell and ligament structure (Yonge, 1980), microstructure of the right valve is not a reliable character for separating these two genera.

Several of the bilaterally asymmetric early shell features characteristic of *A. simplex* are seen in other pteriomorphs common in the Northwestern Atlantic. Prodissoconch II specimens of *Crassostrea virginica* (Gmelin)

and *Ostrea edulis* L. show greater convexity and umbonal protrusion in the left valve than in the right valve (Carriker and Palmer, 1979; Carriker *et al.,* 1980; Waller, 1981). Convexity of right and left valves is nearly equal through late larval stages of *Argopecten irradians* (Lamarck) (Waller, 1976); although in *Placopecten magellanicus* (Gmelin), the left valve is slightly deeper than the right valve, and the left umbo projects further than the right umbo (Merrill, 1961; Culliney, 1974). In early postlarval specimens of these visibly inequivalve species, shell height is greater in the left valve, which is the attached valve in ostreids and the upper valve in pectinids and anomiids (Fig. 26).

Microstructure of early postlarval shells of these species differs in right and left valves. Both valves of the early dissoconch of *C. virginica* and *O. edulis* have a predominant inner foliated layer; however, relative thickness of the outer layer, as well as size of its component prisms, differs in right and left valves of both species (Carriker and Palmer, 1979; Carriker *et al.,* 1980; Waller, 1981). In *A. irradians* and *P. magellanicus* postlarvae, foliated calcite comprises most of the shell; the thin outer layer of prismatic calcite present in the right valve is absent in the left valve (Merrill, 1961; Waller, 1976, 1978). Bilateral asymmetry in shell microstructure is most extreme in the early dissoconch of *A. simplex* as microstructures

**Figure 21.** Crurum and byssal foramen of the right valve after supradorsal union of shell margins. Scale bar = 1.0 mm. BF, byssal foramen; CR, crurum.
**Figure 22.** Exterior surface of the crurum. Scale bar = 50 μm. PRO, prodissoconch; IL, inner layer of the ligament.
**Figure 23.** Exterior surface of prismatic layers of the crurum. Scale bar = 5 μm.
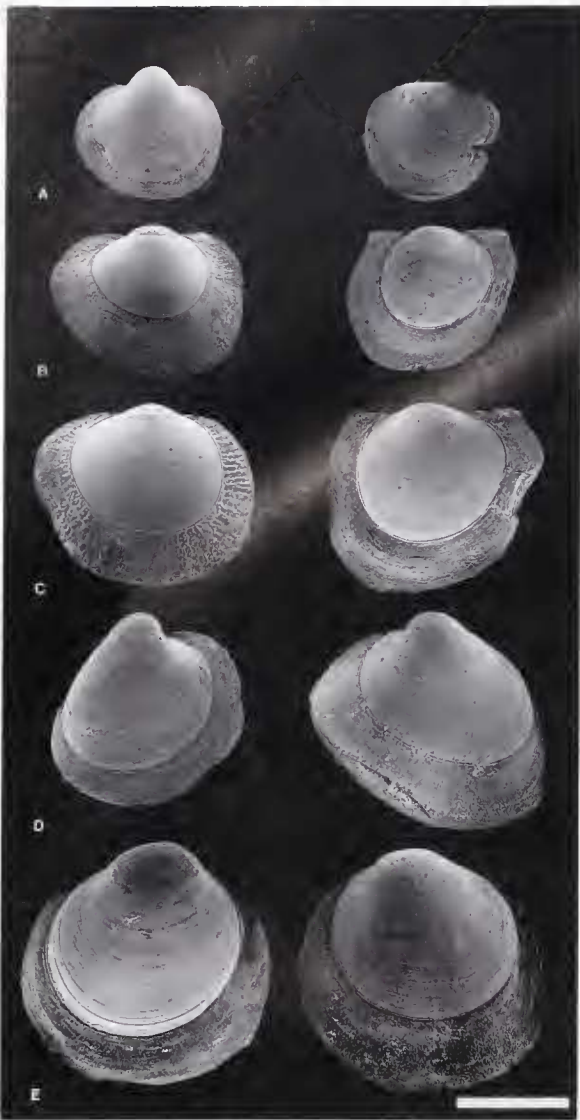
**Figure 26.** Scanning electron micrographs of the exterior surface of disarticulated valves of early postlarval specimens of A. *Anomia simplex*, B. *Argopecten irradians*, C. *Placopecten magellanicus*, D. *Crassostrea virginica*, and E. *Ostrea edulis*. Scale bar = 200 µm. Note marked morphological differences between right and left valves. Left valves are on the left, and right valves are on the right.

of both inner and outer layers differ in right and left valves.

## Acknowledgments

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